

Department of Ecology and Ecotoxicology, Vrije Universiteit, Amsterdam, The Netherlands

Distributional ecology of forest floor Collembola (Entomobryidae) in the Netherlands

J. J. VEGTER, P. DE BIE and H. DOP

With 7 figures

(Accepted: 87-03-20)

1. Introduction

In most terrestrial ecosystems a large number of small arthropod species are involved in decomposition processes. Whether these species are organized in distinct decomposer communities is poorly understood. Community composition, in particular in Collembola, is only weakly related to plant communities (SZEPTYCKI 1967; WALLWORK 1970; HÅGVAR 1982), and abundance of the constituent species seems to vary continuously in relation with successional stages of the vegetation (KACZMAREK 1975; USHER *et al.* 1982), soil moisture regime (KACZMAREK 1975; VEGTER & JOOSSE in prep.), soil fertility (HÅGVAR 1982) and humus type (PONGE 1980, 1983).

In forest floor communities, population density of the more important Collembola species is more or less constant from year to year (VEGTER & JOOSSE, in prep.). Little is known however, about the factors that contribute to the prolonged coexistence of these species. A low degree of food specialization seems to exclude classical food-niche differences as a possible explanation (ANDERSON & HEALEY 1972; ANDERSON 1975). Of course numerous other factors including spatial (VEGTER 1983) and temporal segregation (LEINAAS & BLEKEN 1983; VEGTER in prep.) may promote coexistence of Collembola species. JACOBS (1979) for instance lists ten hypothetical mechanisms to account for the extended coexistence of two related *Daphnia* species in a German subalpine lake.

As local communities might consist of regularly co-occurring species and more opportunistic, non-equilibrium satellite species (CASWELL 1978; HANSKY 1982; BROWN 1984) a study of resource partitioning or other coexistence mechanisms should concentrate on those species that are regularly co-occurring. Some information on geographical distribution of forest floor Collembola in the Netherlands is given by BUITENDIJK (1941) and ELLIS (1974), but at present no systematic study of the degree of co-occurrence of these species has been carried out. The present paper will analyze species composition in entomobryid communities from a large number of woodland areas throughout the Netherlands in order to detect the presence of community differentiation and to identify the species that are regular members of these communities.

2. Methods and materials

In July and August 1979, 49 woodland areas were sampled in a single survey. The locations of these sampling sites are shown in fig. 1. At each site the more important habitat characteristics were recorded such as type of litter, humus type and soil type. These data were used to classify habitats into different types in order to detect habitat preferences of the various entomobryid Collembola species.

Entomobryid Collembola were collected from the litter layer, lower parts of tree trunks, fallen branches and behind loosened bark by means of battery driven aspirators. Three



Fig. 1. Location of the sampling sites and major soil types in the Netherlands.
 ... sand; □ clay; /// löss (loam); other soils

people collected the animals in each site during 20 min, along three 10 m transects. This method aimed at establishing the presence or absence of a species.

A crude estimate of abundance of the more common species was obtained by sampling the litter layer with three soil cores (bore: 30 cm), which were extracted in an enlarged Tullgren-Berlese apparatus.

In order to detect association (or segregation) between species, and between species and types of habitat, a number of statistical tests are applied to the data. First, the frequency distribution of the number of species found at each sampling site is compared with a binomial distribution which is to be expected when there is no association or segregation. This procedure is known as the S-test (BARTON & DAVID 1959; PIELOU 1974). The goodness of fit of the binomial distribution is evaluated with the G-test (SOKAL & ROHLF 1969), a variant of the χ^2 -test.

Second, associations between species pairs are investigated with a G-test for independence in 2×2 tables, using presence and absence data. This test is less reliable for very common and very scarce species and in this paper it is not used if any expected frequency in the 2×2 table is less than five. For common species, abundance as estimated from the soil-cores is classified in two categories to permit a test for association with the G-test.

Because a large number of 2×2 tables are tested, a number of species combinations will show significant G-values by chance alone. This problem is circumvented by the application of a supercritical Chi-square value for significance testing (PIELOU 1974), which is the critical

value of Chi-square at the $5/n\%$ probability level, where n is the number of species combinations tested.

Apart from significance testing, the G-statistic can also be applied in detection, in order to bring out patterns and relationships to be investigated in future studies. The critical value at 5% probability level is then used to judge whether a species combination or a relation of a species with a particular habitat type deserves further attention.

3. Results

Fifteen species of entomobryid Collembola, belonging to five genera were found in this survey. These species are listed in table 1 with their frequency of occurrence and their abbreviated names. Species with a high frequency of occurrence are also the dominant species in most woodlands (fig. 2). In the rarer species, abundance seems to be relatively independent of frequency of occurrence. Species like *O. villosa* (OV) and *H. nitidus* (HN) in particular have a relatively high abundance in a restricted number of woodlands.

The number of entomobryid species per woodland area has been arranged in a frequency histogram in fig. 3 (large white bars), which is compared with a fitted binomial distribution (small black bars). The hypothesis that entomobryid species are independently distributed is rejected. An excess of relatively species rich woodlands is found, indicating an overall aggregation of species.

Table 1. List of entomobryid Collembola species found in this survey

Species	Abbreviation of species names	Frequency of occurrence in the sites
<i>Entomobyra nivalis</i> (LINNÉ)	EN	29
<i>Entomobrya cortalis</i> (NICOLET)	EC	11
<i>Entomobrya albocincta</i> (TEMPLETON)	EA	10
<i>Entomobrya muscorum</i> (NICOLET)	EMS	4
<i>Entomobrya multifasciata</i> (TULLBERG)	EMF	4
<i>Tomocerus flavescens</i> (TULLBERG)	TF	38
<i>Tomocerus minor</i> (LUBBOCK)	TM	26
<i>Tomocerus longicornis</i> (MÜLLER)	TL	21
<i>Tomocerus vulgaris</i> (TULLBERG)	TV	3
<i>Orchesella cincta</i> (LINNÉ)	OC	45
<i>Orchesella flavescens</i> (BOURLET)	OF	10
<i>Orchesella villosa</i> (GEOFFROY)	OV	9
<i>Lepidocyrtus lignorum</i> FABRICIUS	LL	48
<i>Lepidocyrtus violaceus</i> LUBBOCK	LV	1
<i>Heteromurus nitidus</i> (TEMPLETON)	HN	4

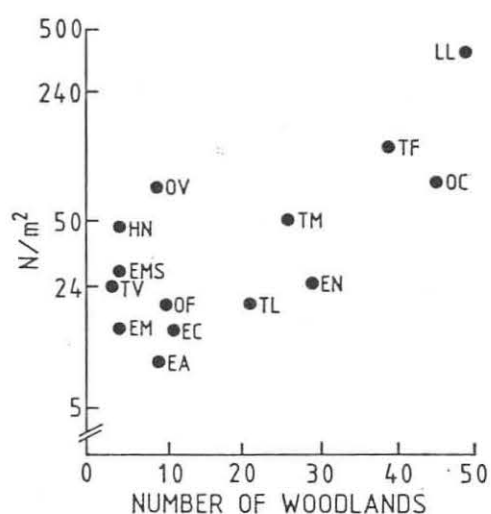


Fig. 2. Relationship between geometric mean abundance of a species, (number per m^2) in the local communities where it is present and the number of sites where the species is found.

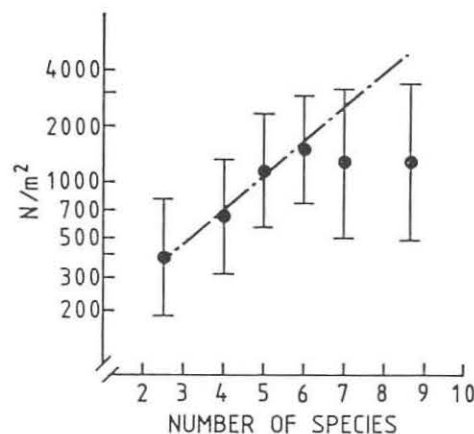
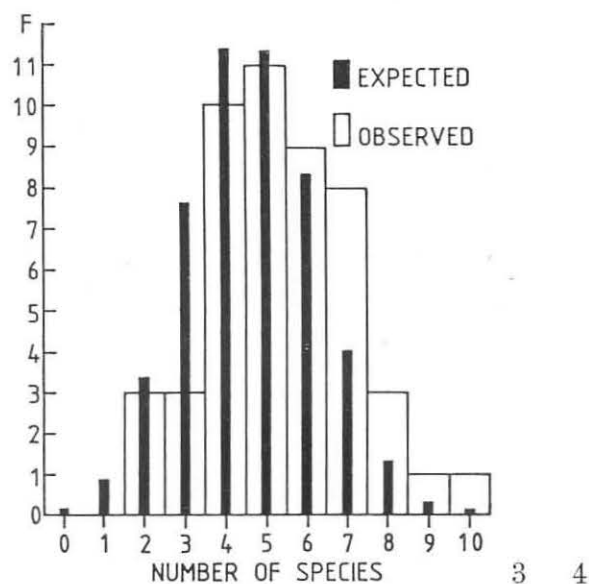


Fig. 3. Observed (white bars) and expected (black bars) frequencies (F) of the number of species per woodland. G-statistic: $G = 11.60$ is significant at the 5% probability level $\chi^2_{0.05}(4) = 9.49$. Expected frequencies less than five have been lumped.

Fig. 4. Relationship between number of species and geometric mean of total number of individuals per m^2 caught in woodlands with a given number of species. Vertical bars indicate 95% confidence intervals for geometric means. Woodlands with two and three species and with more than eight species are lumped.

An underlying cause for this aggregated pattern might be found in differences in productivity or favourability between sites, reflected by the number of individuals caught. As is shown in fig. 4, more individuals are found in woodland areas with more species. As indicated by the dashed lines in this figure, an exponential relationship is observed for assemblages up to six species. In species richer areas which are mainly located in the eastern part of the Netherlands, see fig. 5, total population density of forest floor Collembola is more or less constant.



Fig. 5. Geographical distribution of species richness; ○: < 5 species; ●: 5 and 6 species; *: > 6 species.

Table 2. Species combinations for which a G-test yielded a significant result at the level of probability of error (p) of 0%

Species pair*)	Association	G-statistic	Significance [%]
LL × TF	+	17.63	0.0026
LL × EC	+	9.98	0.16
TF × TL	+	7.57	0.6
TL × EC	+	5.21	2.3
TM × EA	—	4.37	3.7

*) Abbreviations explained in Table 1.

The results presented so far concern overall patterns, and it is therefore interesting to examine the constituent pairwise associations between species and between species and habitat types. In these analyses the more common species were classified in abundance categories (more or less than 100 individuals caught in soil cores for *L. lignorum* and more or less than 10 individuals for *O. cincta* and *T. flavescens*). The remaining species were classified according to presence and absence.

Out of the 105 possible species combinations, 21 species pairs yielded 2×2 tables with expected frequencies larger than 5. Species combinations for which a G-test yielded a significant result at the ordinary 5% probability level are listed in Table 2. As could be expected from the result of the S-test (fig. 3), positive associations do prevail, two of which can even be judged significant at the supercritical probability level of $5/21\% = 0.24\%$.

Whether positively associated species pairs tend to occur in similar habitat types is examined below. First, habitats were classified according to soil type. Because this habitat characteristic is dependent on the location of the study site, this way of classifying habitats is also a geographical and a climatological one. Second, habitats were classified according to

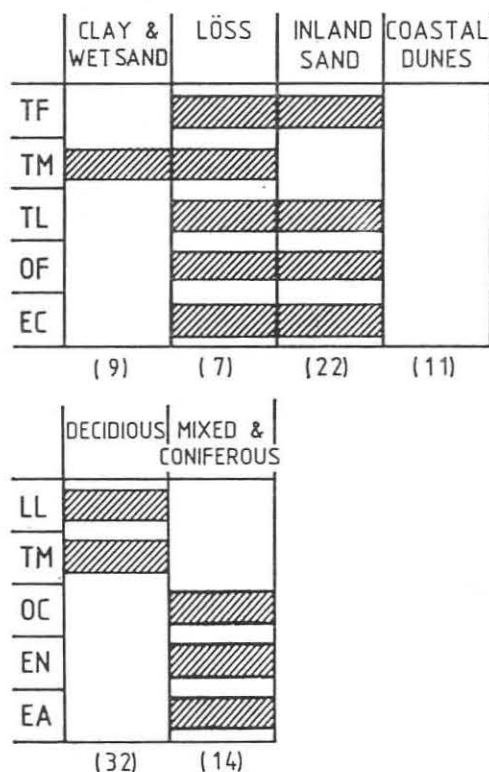


Fig. 6. Habitat type preference. Black bars indicate that the species is more abundant (TF) or found more often in the habitat type considered, judged by a significant G-statistic ($\alpha = 5\%$). In parentheses the number of habitats in each category is given.

Fig. 7. Litter type preference. Black bars indicate that the species is more abundant or found more often in coniferous or deciduous woodland, judged by a significant G-statistic ($\alpha = 5\%$). In parentheses the number of habitats in each category is given. **Erratum:** DECIDIOUS should be read DECIDUOUS.

litter type, that is deciduous woodlands are contrasted with coniferous and mixed woodlands. The results of these analyses are given in fig. 6 and 7. The black bars indicate that a species is found more often in a given habitat type, judged by a significant G-value at the 5% probability level.

When the pairwise associations between species (table 2) are compared with results of the latter two analyses it appears that the positive associations of TF and EC with TL are explained by similarities in habitat type preference in contrast to the associations involving *L. lignorum*. Differences in litter type preference clearly explain the negative association between TM and EA.

4. Discussion

Forest floor collembola communities, if such distinct entities exist at the scale of a local woodland area, must be very similar, in agreement with conclusions reached by HÅGVAR (1982), SZEPTYCKI (1967) and KACZMAREK (1973, 1975). The existence of distinct Collembola communities was already questioned by NOSEK (1963), whereas DUNGER (1975) speculated that Collembola communities should coincide with plant communities. An earlier attempt to classify Collembola communities was made by GISIN (1943), but his system of synusiae deals with very broad habitat categories such as open field versus woodland or with differences in vertical distribution such as litter-dwelling vs. tree-dwelling species.

A more realistic view on forest floor Collembola, proposed by KACZMAREK (1975) is that we are basically dealing with the same community everywhere. A woodland community in the Netherlands might thus simply consist of *L. lignorum*, *O. cincta*, *T. flavescens* and *E. nivalis*, with *T. minor* becoming more important in the moister clay soil habitats, and additional scarce species dependent on soil and litter type. In agreement with results of a previous study (VEGTER & JOOSSE in prep.), the litter type preferences of *T. minor*, *O. cincta*, *E. nivalis* and *E. albocincta* could to some extent be expected from the large differences in drought sensitivity between *T. minor* and the other species (VERHOEF & WITTEVEEN 1980; VEGTER & HUYER-BRUGMAN 1983). The difference in soil type preference between *T. flavescens* and *T. minor* is unrelated to differences in drought tolerance (VEGTER & HUYER-BRUGMAN 1983). Whether interspecific interactions or other important factors such as the presence of clay favouring *T. minor* (cf. TOUCHOT *et al.* 1983) are involved is at present unknown. It is also interesting to note that drought tolerant *Entomobrya* species, which seem well adapted to a wide range of habitats, are among the less common and less abundant species.

Several recent studies demonstrate a positive relationship between distribution and abundance among ecologically similar species (HANSKY 1982; BOCK & RICKLEFS 1983; BROWN 1984). In order to provide some explanation, BROWN (1984) pointed out that those species that can attain high densities in some places should be able to do so in many other sites in a given region, because important environmental conditions tend to be fairly similar over large areas. Therefore this positive relationship implies a low degree of community differentiation. HANSKY (1982) used the relation between local abundance and geographic distribution to derive a model which results in a bimodal frequency distribution of species occurrences, and he suggests that communities are made up of two types of species: core species, inhabiting virtually all habitats and less abundant satellite species, occurring in a few habitats.

Occasionally, such a bimodal frequency distribution of species occurrences is observed (see HANSKY 1982), but this bimodality will only rarely be very clear, since there are in fact two types of rare and less abundant species. The first type are species that are "core" species elsewhere and have the centers of their distribution outside the region sampled. They are less abundant because population density declines from the center to the periphery of a geographical range (HENGEVELD & HAECK 1982). The species *O. flavescens*, *T. vulgaris*, and *E. muscorum* which are more abundant in areas with a continental climate, for instance Germany, and the species *O. villosa* and *H. nitidus* which are not classified as woodland species by GISIN (1943), might be examples of this type. The second type consists of species

with a restricted geographical distribution that have their centers close to or within the region sampled. Moreover, the relation between frequency of occurrence and local abundance is likely to be different in these two types. Therefore a joint relation for a mixture of these types might also be less prominent. The results from this study seem to substantiate this. Only the more common species exhibit a clear relationship between local abundance and commonness.

If species are somehow energetically linked through their resources, the inclusion of another species in a local assemblage might require a proportional increase in population densities of species already present, which will yield (according to ODUM, CANTLON & KORNICHER 1960) an exponential relationship between total number of individuals and number of species. As was noted by MAY (1975 b) this relationship leads to linear log-abundance rank plots, that appear to characterize the forest floor collembola communities studied by VEGTER & JOOSSE (in prep.). In the present study woodlands with less than six species showed an exponential relation between total number of individuals and number of species. This feature, observed from a large number of habitats, is in agreement with the above mentioned ODUM-CANTLON-KORNICHER distribution which was formulated for a single community. This agreement again suggests that communities in different woodlands are in fact large subsets from one and the same community. In woodlands inhabited by more than six species the total number of individuals seems to be unrelated to the number of species. Apparently, community structure in species rich woodland areas is different, as was also found by VEGTER & JOOSSE (in prep.). As the majority of species rich areas is located in the eastern part of the Netherlands they might be subject to more frequent colonizations, especially by species having their centers of distribution in the more continental parts of Europe.

The low degree of community differentiation in forest floor Collembola is also reflected in the result of the S-test. The frequency distribution of the number of species found in a local woodland area is aggregated. Whether this aggregated pattern is generated by mutualistic interactions between species or by site differences or both is an important question, that cannot be answered without additional information (PIELOU & PIELLOU 1968). The positive relation between the logarithm of total abundance of individuals and the number of species present in a woodland area suggests that differences in environmental quality or productivity are important.

In addition to differences in favourability between woodland areas a few large positive pairwise associations between species appear to contribute disproportionately to the overall pattern of species aggregation. The pairwise associations between *L. lignorum* and *T. flavescens*, and *T. longicornis* and *T. flavescens* are particularly interesting because these species have very different phenologies, which might lead to different peaks and lows in population numbers during a season. *L. lignorum* is a bivoltine species with a high population peak early in spring due to the synchronized emergence of hatchlings from wintered eggs (LEINAAS & BLEKEN 1983). Reproduction of *T. flavescens* starts much later (BELLINGER 1954, PETERSEN 1960), whereas its congener *T. longicornis* is a univoltine species that winters in the egg stage and hatches early in spring. Coexistence in these species might be facilitated by seasonal differences in resource utilization. LEINAAS & BLEKEN (1983) already suggested that the dominance of *L. lignorum* in collembola communities might be attributed to its distinct phenology. This seasonal mode of resource partitioning will be investigated in more detail in a forthcoming paper.

5. Acknowledgements

The authors wish to thank "Staatsbosbeheer", "de Vereniging tot Behoud van Natuurmonumenten" and "de Provinciale Landschapsstichtingen" for their kind permission to sample woodlands in Dutch nature reserves, and Prof. Dr. E. N. G. JOOSSE and Dr. G. ERNSTING for valuable comments on earlier drafts of this paper.

6. Literature

- ANDERSON, J. M., 1975. The enigma of soil animal species diversity. In: VANĚK, J. (ed.), Progress in Soil Zoology. Proc. 5th Int. Coll. Soil Zool. Prague (1973), pp. 51—58.
- & J. N. HEALEY, 1972. Seasonal and interspecific variation in the major components of the gut content of some woodland Collembola. J. Anim. Ecol. **41**, 359—368.
- BARTON, D. E., & F. N. DAVID, 1959. The dispersion of a number of species. J. R. Statist. Soc. B **21**, 190—194.
- BELLINGER, P. F., 1954. Studies of soil fauna with special reference to the Collembola. Connecticut agric. exp. station bulletin **583**, 1—67.
- BROWN, J. H., 1984. On the relationship between abundance and distribution of species. Am. Nat. **124**, 255—279.
- BITENDIJK, A. M., 1941. Collembola. Fauna Ned. **11**, 1—99.
- BOCK, C. E., & R. E. RICKLEFS, 1983. Range size and local abundance of some North American songbirds: a positive correlation. Am. Nat. **122**, 295—299.
- CASWELL, H., 1978. Predator-mediated coexistence: a non-equilibrium model. Am. Nat. **112**, 127—154.
- DUNGER, W., 1975. On the delimitation of soil microarthropod coenoses in time and space. In: VANĚK, J. (ed.), Progress in Soil Zoology. Proc. 5th Int. Coll. Soil Zool. Prague (1973), pp. 43—49.
- ELLIS, W. N., 1974. Ecology of epigeic Collembola in the Netherlands. Pedobiologia **14**, 232—237.
- GISIN, H., 1943. Ökologie und Lebensgemeinschaften der Collembolen im Schweizerischen Exkursionsgebiet Basels. Revue suisse Zool. **50**, 131—224.
- HÅGVAR, S., 1982. Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. Pedobiologia **24**, 255—296.
- HANSKY, F., 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos **98**, 210—221.
- HENGVELD, R., & J. HAECK, 1982. The distribution of abundance. I. Measurements. J. Biogeogr. **9**, 303—316.
- JACOBS, J., 1979. Concluding remarks: On the difficulty to reconcile theories with facts. Fortschr. Zool. **25**, 403—409.
- KACZMAREK, M., 1973. Collembola in the biotopes of the Kampinos National Park distinguished according to the Natural succession. Pedobiologia **13**, 257—272.
- 1975. An analysis of Collembola communities in different pine forest environments. Ekol. Pol. **23**, 265—293.
- LEINAAS, H. P., & E. BLEKEN, 1983. Egg diapause and demographic strategy in *Lepidocyrtus lignorum* FABRICIUS (Collembola, Entomobryidae). Oecologia (Berlin/West) **58**, 194—199.
- MAY, R. M., 1975. Patterns of species abundance and diversity. In: CODY, M. L., & J. M. DIAMOND (eds.), Ecology and evolution of communities. Harvard University Press, Cambridge, Mass., pp. 10—120.
- NOSEK, J., 1963. Zur Kenntnis der Apterygoten der Kleinkarpatischen Wald- und Dauergrünlandböden. Pedobiologia **2**, 108—131.
- ODUM, H. T., J. E. CANTLON & L. S. KORNICHER, 1960. An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution, and the meaning of a species variety index. Ecology **41**, 395—399.
- PETERSEN, H., 1980. Population dynamic and metabolic characterization of Collembola species in a beech forest ecosystem. In: DINDAL, D. E. (ed), Soil biology as related to land use practices. Proc. 7th Int. Coll. Soil Zool. Syracuse (1979), pp. 1306—1333.
- PIELOU, D. P., & E. C. PIELOU, 1968. Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (BULLIARD) FRIES. J. theor. Biol. **21**, 202—216.
- PONGE, J. F., 1980. Les biocénoses de la forêt de Sénart. In: PESSON, P. (ed.), Actualités d'écologie forestière. Gauthier-Villars, Paris, pp. 151—176.
- 1983. Les collemboles, indicateurs du type d'humus en milieu forestier. Résultats obtenus au Sud de Paris. Acta Oecologia, Oecol. Gener., **359**—374.
- SOKAL, R. R., & F. J. ROHLF, 1969. Biometry. W. H. Freeman & Co., San Francisco.
- SZEPTYCKI, A., 1967. Fauna of the springtails (Collembola) of the Ojców National Park in Poland. Acta Zool. Cracov **12**, 219—280.
- TOUCHOT, F., G. KILBERTUS & G. VANNIER, 1982. Role d'un collembole (*Folsomia candida*) au cours de la dégradation des litières de charme et de chêne en présence ou en absence d'argile. Proc. 6th Int. Coll. Zool. Louvain-la-Neuve.
- USHER, M. B., R. G. BOOTH & K. E. SPARLIES, 1982. A review of progress in understanding the organisation of communities of soil arthropods. Pedobiologia **23**, 126—144.
- VEGTER, J. J., 1983. Food and habitat specialization in coexisting springtails (Collembola, Entomobryidae). Pedobiologia **25**, 253—262.
- & F. A. HUYER-BRUGMAN, 1983. Comparative water relations in Collembola: transpiration, desiccation tolerance and effects of bodysize. Proc. 8th Int. Coll. Zool. Louvain-la-Neuve (1982).

- VERHOEF, H. A., & J. WITTEVEEN, 1980. Water balance in Collembola and its relation to habitat selection; cuticular water loss and water uptake. *J. Insect. Physiol.* **26**, 201—208.
- WALLWORK, J. A., 1970. *Ecology of soil animals*. McGraw-Hill, London.

Address of authors: J. J. VEGTER (corresponding author), Department of Ecology and Ecotoxicology, Vrije Universiteit Amsterdam, De Boelelaan 1087, Amsterdam-Buitenveldert, NL-1007 MC.

Synopsis: *Original scientific paper*

VEGTER, J. J., P. DE BIE & H. DOP, 1988. Distributional ecology of forest floor Collembola (Entomobryidae) in the Netherlands. *Pedobiologia* **31**, 65—73.

Fifteen species of entomobryid Collembola, belonging to five genera were found in this survey. Species with a high frequency of occurrence are also the dominant species in most woodlands. In the rarer species, abundance seems to be relatively independent of frequency of occurrence. Species like *Orchesella villosa* and *Heteromurus nitidus* in particular have a relatively high abundance in a restricted number of woodlands.

The hypothesis that entomobryid species are independently distributed is rejected. An excess of relatively species rich woodlands is found, indicating an overall aggregation of species. An underlying cause for this aggregated pattern might be found in differences in productivity or favourability between sites, reflected by the number of individuals caught. More individuals are found in woodland areas with more species. An exponential relationship is observed for assemblages up to six species. In richer areas, which are mainly located in the eastern part of the Netherlands total population density of forest floor Collembola is more less constant.

Key words: Collembola, Entomobryidae, population density, aggregation, distribution, ecology, forest floor, Netherlands.